PROC. R. SOC. VICT. vol. 95, no. 3, 133-138, September 1983

THE POTENTIAL FOR BREEDING SALT-TOLERANT PLANTS

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Abstract: The potential for selecting and breeding of plants with increased tolerance to salinity appears to be good because of the existence of heritable variation for tolerance between genera and species, within species and within cultivars. Information on the genetic control of salt-tolerance would help in its selection and breeding. However, few studies have yet been conducted on the heritability and inheritance of tolerance in different plant species.

Although intraspecific variation for salt-tolerance affords the most readily accessible source of genetic variation for selecting and breeding for increased tolerance, many plant breeding techniques exist which may offer breeders with a means of producing greater variation for tolerance than might otherwise be available in a crop species, e.g., chromosome manipulation, somatic hybridization and plant cell culture.

In conjunction with further research on the genetic control of salt-tolerance in a crop species, research on the physiological basis of tolerance, its variation with ontogeny and the influence of the environment should lead to increases in the tolerance of crop species through selection and breeding.

PLANT ADAPTATION TO HIGH LEVELS OF MINERAL ELEMENTS IN SOILS

High levels of mineral elements in the soil can often cause serious limitations to agricultural production and land development. Approaches such as fertilizer application, soil drainage and improved irrigation management have been used in attempting to overcome these limitations. Another approach is the selection and breeding of plants for greater tolerance of the mineral element and hence greater productivity in such areas.

The potential for selecting and breeding of plants for increased tolerance of high levels of mineral elements in the soil appears to be good because of the reported existence of heritable variation for such tolerance in a large number of plant species (Humphries & Bradshaw 1976, Reid 1976, Foy & Fleming 1978, Epstein 1983). For example, variation in tolerance to heavy metals has been reported between cultivars of such species as barley and wheat (Foy *et al.* 1965), rice (Howeler & Cadavid 1976), lucerne (Ouellette & Dessureaux, 1958) and soybean (Armiger *et al.* 1968) as well as between plants in ecotypes of certain grass species (Wu *et al.* 1975). Such variation has been shown to be genetically controlled, as for instance, tolerance to aluminium in barley which is conferred by a single dominant gene (Reid 1970) and in wheat by one or more major and several modifying genes (Kerridge & Kronstad 1968). Tolerance to high levels of available copper and zinc in *Agrostis tenuis* is highly heritable (McNeilly & Bradshaw 1968, Gartside & McNeilly 1974) and additive genetic variation for tolerance to high levels of copper has been shown within tolerant ecotypes of *Agrostis stolonifera* (Wu *et al.* 1975).

The occurrence of apparently wide genetic variation in plants for tolerance to high levels of elements such as aluminium and zinc in the soil is paralleled by variation between species, cultivars and individual plants for tolerance to high levels of soil salinity.

VARIATION IN SALT-TOLERANCE OF PLANTS

Considerable research effort has been directed towards identifying plant species and varieties that are tolerant of salinity. Ramage (1980) noted that over 1500 species have been used for studying plant responses to salinity and that over 50 crop species have been evaluated for varieties that exhibit salt-tolerance, including cereal, fibre, oilseed and vegetable crops, and forage grasses and legumes.

Halophytic plant species are considerably more salt-tolerant that glycophytic species (Flowers *et al.* 1977). They can survive and complete their life cycles at electrolyte concentrations up to 600 mM with an optimum concentration for growth in the region of 20 to 500 mM (Flowers *et al.* 1977) compared with glycophytes which do not show this optimum effect and may survive up to only 300 to 350 mM (Greenway & Munns 1980). Halophytes, however, are in most cases of limited value for agricultural production and for that reason, the following discussion is limited to glycophytes.

Information from many studies is available on comparative levels of tolerance between a large number of species (e.g. Maas & Hoffman 1977). Studies of intraspecific variation for salt-tolerance have revealed large differences in tolerance, such as within crested wheatgrass (Dewey 1962), tall wheatgrass (Shannon 1978), soybean (Abel & McKenzie 1964) barley (Greenway 1962) and rice (Akbar *et al.* 1972). In some studies, however, little or no intraspecific variation in tolerance has been found, as for example, beans (*Phaseolus vulgaris*) (Bernstein & Ayers 1951) and lettuce (*Lactuca sativa)* (Ayers *et al.* 1951). The absence of intraspecific variation may be a reflection of a limited number of cultivars being tested, or possibly that little variation for this character has been incorporated in the domestication and recent breeding of the species. Variation in salt-tolerance has also been found between different populations of species occurring naturally in saline and non-saline habitats. For instance, Hannon and Bradshaw (1968) found significant variation in salt-tolerance between different ecotypes of both *Festuca rubra* and *Agrostis stolonifera*.

There may also be variation for salt-tolerance between individuals in a population of a species. This might be expected to be larger in an open-pollinated, compared with self-pollinated, species and it has been found in open-pollinated cultivars of cotton (Maliwal *et al.* 1975), sugar beet (Ulrich 1961) and lucerne (Dobrenz *et al.* 1981).

SELECTION AND BREEDING FOR SALT-TOLERANCE

Heritability and Inheritance of Salt-tolerance

A primary requisite in selecting and breeding for salt-tolerance is genetic variation for tolerance in the gene pool of the species for which increased tolerance is required. Interspecific, intraspecific and intracultivar variation for tolerance provides scope for selecting for its improvement. However, information on the genetic control of tolerance would help in its selection and breeding. A knowledge of the level of heritability and the inheritance of salt-tolerance in a species can help in devising a selection strategy for tolerance, such as the intensity and number of cycles of selection necessary to effect significantly increased tolerance. It could also facilitate the incorporation of tolerance in commercial cultivars from related species or lines by hybridization and selection.

If sufficient genetic variation for tolerance exists in a species and its heritability is high, then large increases in tolerance could be expected from selection. However, if the heritability is low, a high selection intensity would be needed even for small responses to selection and large responses may, therefore, be difficult to achieve. In the latter case an alternative species may be considered that has either, or both, an inherently high level of tolerance, and variation for tolerance so that increases might be expected through selection.

Knowledge of the heritability and inheritance of salt-tolerance in most agricultural plant species is generally lacking because few studies have yet been conducted in these areas. Dewey (1962), after evaluating the salt-tolerance of 60 strains of *Agropyron desertorum*, proposed a recurrent selection and breeding program for increasing its salt-tolerance. Abel and MacKenzie (1964) found variation in salt-tolerance between soybean cultivars and Abel (1969) found that tolerance in soybean was controlled by a single dominant gene. Hunt (1965) demonstrated that mature plant salt-tolerance in *Agropyron intermedium* was heritable with a parent-progeny correlation coefficient (r) of 0.83 and a coefficient of determination, r^2, of 68 per cent. The F_1 hybrids of salt-tolerant and -sensitive rice cultivars were more tolerant than parental lines (Akbar & Yabuno 1977) while the F_2 exhibited a wider range of variation than the parents, and tolerant progenies were selected from F_3 and F_4 generations (Akbar *et al.* 1977, Akbar & Yabuno 1977). Two types of sterility were induced by salinity in rice and resistance to a delayed-type panicle sterility was dominant and controlled by a small number of genes (Akbar & Yabuno 1977). Norlyn (1980) found the ability of barley to yield under salinity was heritable and that its genetic control was complex. Dobrenz *et al.* (1981) utilised variation within a lucerne cultivar and obtained increased salt-tolerance during germination from selection.

Sources of Salt-tolerance Beyond Intraspecific Variation

Although significant levels of intraspecific variation for salt-tolerance afford the most readily accessible sources of genetic variation for selecting and breeding for increased tolerance, some agricultural species either possess very little variation for tolerance or relatively low levels compared with other species. For such species consideration should be given to other ways in which higher levels of tolerance might be obtained. A number of these possible methods are outlined below. However, the success from using the following approaches depends largely on the possiblilty that salt-tolerance in plants is under particulate gene control.

Exploitation of alien variation for tolerance

Those salt-tolerant species and genera related to a crop plant which exhibit high levels of chromosome pairing with it could contribute useful sources of tolerance to the crop species through interspecific and intergeneric hybridization. It is possible that within the gene pool of an agricultural species, amongst its "wild" and "weed" related species, significant amounts of variation for this character may exist. For instance, little variation for tolerance was found in the commercial tomato *Lycopersicon esculentum*, but crosses with the salt-tolerant related species *L. cheesmanii*, followed by several backcrosses to *L. esculentum*, gave plants with higher levels of tolerance than the commercial tomato, although with reduced fruit size (Rush & Epstein 1976).

In many interspecific crosses, fertilisation and early embryo development occurs but embryo death may result from malnutrition due to endosperm failure (Raghaven 1977). Embryo culture, involving the excision of such embryos and their culture on nutrient media, has been used successfully for interspecific hybrids in cotton, barley, tomato and rice, and with intergeneric hybrids of *Hordeum* and *Secale*, *Triticum* and *Secale*, and *Tripsacum* and *Zea* (Yeung *et al.* 1981). The technique may, therefore, broaden the range of cross compatibility between crop plants and their related species and genera for breeding for salt-tolerance by providing access to a greater range of variation for this character.

Chromosome manipulation techniques, such as chromosome addition, substitution and translocation provide the potential to transfer salt-tolerance into the genome of a crop plant from species and genera related to the crop species, but whose chromosomes do not pair, or show only little pairing with those of the crop plant. The successful use of these techniques in plant breeding, as for instance the transfer of stem, leaf and stripe rust resistance from *Agropyron intermedium* into wheat by chromosome addition, substitution and translocation (Wienhues 1966) indicate the feasibility for their successful use in incorporating salt-tolerance in crop plants. One possibility for the application of these techniques is the transfer of the high level of salt-tolerance of *A. elongatum* into wheat. Success from the use of such techniques will depend in part on the expression of salt-tolerance of the related species being maintained in the genetic background of the crop plant, and on the absence of deleterious effects of the substituted or added chromosome or translocated segment bearing salt-tolerance on the adaptability and yield of the crop plant.

Somatic hybridization, resulting from the fusion of protoplasts derived from different species, also offers the potential for transferring genetic information for salt-tolerance from one species to another. Smith *et al.* (1976) recovered mature hybrid plants between two species of tobacco, *Nicotiana glauca* and *N. langsdorfii*, by protoplast fusion. However, there are few other reports where this technique has resulted in hybrids.

Other techniques useful for interspecific hybridization are discussed by Stalker (1980), some of which may be useful for transferring salt-tolerance to an agricultural species from other species within its gene pool.

Induction of variation for salt-tolerance

The induction of variation in salt-tolerance by mutagenic agents such as chemical or radiation treatments, offers the potential for providing new sources of variation for this character. Induced mutation techniques enable the full range of naturally occurring mutations to be produced plus those that have been lost through natural selection, and possibly new forms of mutant expression. These techniques have been used to produce new sources of genetic variation for characters such as yield, and pest and disease resistance in a number of agricultural species (Anon 1970). For example, Gustafsson (1941) induced cold resistant barley mutants by irradiating seeds with x-rays.

Plant cell cultures, which can be derived from virtually any part of a plant, including root or stem sections, cotyledons and leaves (Scowcroft 1977), afford the opportunity of screening large numbers of cells for salt-tolerance. Dix and Street (1975) used callus cultures derived from petioles of *Nicotiana sylvestris* and *Capsicum annuum* to select cell lines capable of growing in liquid media containing one and two per cent (w/v) NaCl. Similarly, Nabors *et al.* (1975) selected cell lines derived from stem sections of *Nicotiana tobacum* which were tolerant of a growth medium containing 1.6 g/l NaCl and Croughan *et al.* (1978) selected a cell line derived from lucerne cotyledon tissue with increased growth under a range of NaCl levels compared with an unselected cell line. To date there is no evidence to judge whether plants regenerated from such tolerant cells are also tolerant to high NaCl concentrations. Success with this technique will depend on whether cell and whole-plant tolerance to NaCl are closely associated. Recent studies by Tal *et al.* (1978), Orton (1980) and Smith and McComb (1981 a, b) found that the growth responses to NaCl of whole plants and callus (from hypocotyl tissue) were very similar for tomatoes, barley, lucerne, white clover, strawberry clover, beans, and sugarbeet.

A further potential benefit of plant cell culture techniques in searching for salt-tolerance is the occurrence of large amounts of genetic variation in plants regenerated from cell cultures which could possibly embrace variation for increased tolerance. For instance, Shepard *et al.* (1980) found significant variation for tuber size, maturity date, photoperiod requirement and resistance to late blight (*Phytophthora infestans*) in somaclonal lines derived from leaf protoplasts in potato. Somaclonal variation has also been demonstrated for rice (Nishi *et al.* 1968), sugarcane (Heinze & Mee 1969), and oats (Cummings *et al.* 1976). Consequently, this technique appears to offer breeders with a means of producing greater variation for tolerance than might otherwise be available in a crop species.

Factors Influencing the Selection and Breeding for Salt-tolerance

While a primary requirement in selecting and breeding for increased salt-tolerance is the existence of heritable variation for it, there are several factors which can influence the level of tolerance in a plant population, which are as follows:

Indices of salt-tolerance

A range of criteria, or indices, have been used in evaluating salt-tolerance in agricultural plants, including percentage germination, shoot dry weight, shoot number, leaf necrosis and seed yield. Different plant characters can exhibit differing responses to salinity, for example Ayers *et al.* (1952) found seed production in barley and wheat was decreased less by salinity than was vegetative growth measured as shoot dry weight. Consequently, the level of salt-tolerance between and within species is likely to vary according to the criteria used to evaluate its effects on growth and productivity.

Stage of growth and tolerance

The influence of salinity on plant growth has been studied as its effects on germination, seedling emergence, seedling and later plant growth, flowering, seed set and vegetative regrowth (of perennials). Salt-tolerance in a plant species appears to vary during its ontogeny. For instance, wheat and barley are more sensitive to salinity during early seedling growth than at germination or during later growth (Ayers *et al.* (1952) while sugar beet is more sensitive to salinity during germination than during other growth stages (Bernstein & Hayward 1958). Because of these differences, some studies have been concerned with selecting for salt-tolerance under saline conditions imposed over the entire growth cycle, as with tomato and barley (Epstein *et al.* 1980). However, if a constant salt concentration is used in such an approach, because of the possible variation in tolerance at different growth stages the selection intensity for tolerance will in consequence vary with stage of growth. Varying the concentration of salt during selection according to the sensitivity of the stage of growth may be a practical alternative. A further option would be to screen separately for tolerance at each stage of growth, allowing a salt concentration during each stage to provide the appropriate selection intensity and permitting additional cycles of selection on those growth stages with relatively low heritabilities for tolerance. Lines selected for tolerance at particular stages of growth could be recombined and their segregates screened for overall tolerance throughout plant growth.

In some species selection for increased salt-tolerance may be necessary at only one growth stage. For instance, sugar beet is highly sensitive to salinity only at germination (Bernstein & Hayward 1958) and selection for tolerance during this stage should remove a limiting step to tolerance throughout its growth.

Knowledge of the physiological basis of salt-tolerance

Reviews by Greenway and Munns (1980), Hsiao (1973), Jennings (1976) and Maas and Nieman (1978) provide an excellent coverage of current knowledge of the physiological basis of the response of plants to salinity. However, limited information is available on the comparative physiology of genetically closely related plants that differ markedly for salt-tolerance. Comparisons have been made between species of a different genus for differences in characters such as ion uptake, organic solute concentrations and ion distribution when grown under high levels of salinity. However, as indicated by Epstein (1980), these differences are to be expected simply on the basis of phylogenetic differences between them. As an alternative, Epstein (1980) proposed that if plant breeders can identify closely related genotypes that differ markedly in salt-tolerance, such as species of one genus or genotypes within a species or cultivar, then such populations would be useful in determining the physiological basis of salt-tolerance in a species. Such studies could provide breeders with physiological or morphological criteria for selecting for increased tolerance. Criteria based on mechanisms that confer tolerance are more likely to be more accurate indices of tolerance than those based on a phenotypic character, such as yield, which are strongly influenced by the environment and can also give inflated estimates of tolerance due to hybrid vigour.

Examples of comparative studies between related genotypes differing in salt-tolerance include that of Abel and MacKenzie (1964) who found differences in tolerance between salt-tolerant and -sensitive soybean cultivars was associated with differences in their ability to exclude chloride ions from the stems and leaves. Rush and Epstein (1976, 1981) found the higher salt-tolerance of the "wild" tomato, *Lycopersicon cheesmanii* ssp *minor*, compared with the commercial *L. esculentum*, was associated with lower levels of total amino nitrogen, specific amino acids and free acidity, and higher shoot concentrations of sodium, while Tal *et al.* (1979) found the tolerant "wild" tomato *L. peruvianum* had half the proline but double the chloride concentration of *L. esculentum*. Hannon and Barber (1972) investigated physiological differences between ecotypes of *Festuca rubra* which Hannon and Bradshaw (1968) had found to differ for salt-tolerance. Tolerance was found to be associated with a greater ability to exclude sodium and chloride ions from the shoots.

Influence of environment

Comparative studies of the salt-tolerance of plants have been conducted under a range of environmental conditions, including different temperatures, humidities, daylengths and light intensities, with plants grown in different growth media, such as water culture and artificially salinized soils. Similarly, a range of salts (e.g. NaCl, Na_2SO_4, KCl, $NaHCO_3$, $MgCl_2$ and $CaCl_2$) have been used to study the influence of salinization on plant growth. Variation in these factors has been shown to influence the level of salt-tolerance in plants (Bernstein & Hayward 1958, Nieman & Poulsen 1971, Bernstein & Francois 1973, Bernstein *et al.* 1974, Nieman & Shannon, 1977, Maas & Hoffman, 1977). Differences in environmental conditions, both root and aerial, between different studies makes it difficult to make close comparisons between their results. For example, many crops seem less tolerant of salinity when grown under hot dry compared with cool humid conditions, although all crops are not equally affected (Maas & Hoffman, 1977). Consequently, environmental factors must be considered when evaluating and selecting for salt-tolerance.

One environmental factor that appears to influence the effect of salinity on plant growth and which is worthy of consideration, particularly in Australia, is low root-zone oxygen concentration. Waterlogging of the soil and salinity can occur together in both irrigated conditions where there are poorly drained soils, and under dryland conditions in saline seeps. Studies of soil-oxygen deficiency and high soil salinity in citrus (Pearson *et al.* 1957), tomatoes (Aubertin *et al.* 1968, West & Taylor 1980b), oats (Abd-El-Kadous 1974), apple trees (West 1978) and beans (West & Taylor 1980a) indicated the compounding effect of soil-oxygen deficiency on that of salinity on plant growth. West and Taylor (1980a) noted "while some agronomically important plants may be reasonably well adapted to either salinity or to oxygen deficiency (waterlogging), there is no information which suggests that these plants are adapted to both conditions together".

Future Prospects for Selecting and Breeding for Increased Salt-tolerance in Agricultural Plants

Genetic variation for salt-tolerance in many agricultural plants appears to be available from a range of different sources. Further research on new plant breeding techniques should further expand the range of available genetic variation for tolerance. Knowledge gained from further research on the physiological basis of tolerance and its variation with ontogeny should permit the refinement of selection and breeding techniques.

It does not appear feasible to breed glycophytic plants with levels of salt-tolerance as high as those of halophytic plants because of basic physiological differences in their response to salinity. Halophytes have the ability to accumulate ions such as sodium and chloride to high internal concentrations while glycophytes respond to salinity basically by ion exclusion (Flowers *et al.* 1977, Greenway & Munns 1980). In breeding glycophytes for salt-tolerance, however, it may be possible to effect, for example, substantial increases in the threshold level of salinity at which significant yield reductions take place or to reduce the yield decline per increment in soil salinity within the range where yield is adversely affected. Such changes would not require a major alteration to an existing physiological mechanism(s) of tolerance, but rather a selection for maximum efficiency of this mechanism(s).

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